SOIL AS THE ENVIRONMENT OF THE INVERTEBRATE TRANSITION FROM THE AQUATIC TO THE TERRESTRIAL LIFE

by

M.S. GHILAROV
of Institute of Animal Morphology
and Commission on Colorado Beetle Problem, Moscow.

The study of the peculiarities of soil as environment enables the solution of cardinal biological problems, in particular those of the phylogenese.

Phylogenetical schemes are mainly based on the data of morphological disciplines, which form the base of modern evolutionary conceptions. The conceptions concerning the origin of terrestrial animal groups from the aquatic ancestors are generally adopted, but the transition pattern from water to land in the course of phylogenese, especially that of the bulk of invertebrates is not elucidated enough. The application of the comparative ecological method, the examination of the possible environmental changes, the study of organism changes in their relation to the environmental conditions may be of the greatest use for elucidating the pattern of this transition.

The most significant differences in existence in water and on land are the different respiration conditions and the danger of desiccation on land. The oxygen content of the air is much higher than that solved in water, the transition of aquatic organisms to the aerial respiration being confronted by the desiccation of respiratory surfaces.

The gas exchange itself in the organs of aquatic respiration, especially in the case of skin respiration, may take place in the air too. The transition of the aquatic forms with the slightly differentiated respiratory organs, in particular of the forms with skin respiration, may be easily imagined as taking place through the medium with water vapors saturated air. Such medium would have enabled the respiration of air oxygen with the minimal loss of water.

For many invertebrate groups such environment providing the gradual adaptation to aerial respiration had, probably, been the soil, which air, according to A.F. Lebedev, 1911, is saturated with water vapors.

Many soil typically terrestrial (s.l.) airbreathing invertebrates (Elaterid, Tipulid larvae) by their physiological properties are similar to the aquatic ones (susceptibility to dessiccation, poikilosmy, orientation by the gradient of dissolved substances, ability to skin respiration, saprophagy, vertical migrations).

The soil as environment resembles the water masses (the high CO_2—content, vertical temperature gradient and its daily and seasonal inversions, the possibility of locomotion in vertical direction, presence of water, etc.).

Many soil scientists have reckoned the bottom for peculiar soils, whereas the hydrobiologists have appreciated the soil water as specific water mass. The differences between the bottoms and soil are especially relative in the case of temporary water masses the given area changing its character in seasonal aspect.

From the ecological viewpoint, the soil as environment which allows airbreathing without the danger of rapid dessiccation is intermediate between the aquatic and the aerial one.

Let us take a view at the occurrence of the representatives of different invertebrate groups (1) in water and on land, appreciating the soil (the litter including) as a peculiar environment. Usually only the water and land habitats are opposed (Hesse, 1924).

All the Protozoa live in water or soil where they are to be found in the water drops or films.

The majority of Turbellaria are aquatic, but some Rhabdocoela and Triclada are transiting to the terrestrial life; the terrestrial ones being characterized just by the soil and litter dwelling. Among the Nemertini—the typically aquatic group—there is a number of soil dwellers (*Geonemertes*). The free living nematodes inhabit marine and fresh water and humid soil. I.N. Filipyev has shown that the marine forms are the most primitive ones. Among the Annelids the bulk of the Polychaeta are marine forms. Though terrestrial Polychaeta have been found by W. Harms, 1934, in the Malay Archipelago and in Provence *Nereis diversicolor* is a soil dweller, like the earthworm (Herzog, 1935). Among the Oligochaets " terricolae "—are soil dwellers, whereas among the more primitive " limicolae " the bulk inhabits fresh water, but there are also some soil inhabiting forms (e.g., Enchytraeidae). Of interest is the example of typically bentical *Tubifex*, adjusted to soil dwelling after the lake drainage.

Among the Arthropods the Crustacea are being characterized by the aquatic life. Only a few Entomostraca (some Harpacticidae) occur in the soil. Among the Malacostraca the more closely adjusted to terrestrial life are the Oniscoidaea which show all the transition stages from the aquatic to terrestrial life. There are even representatives of the desert fauna (*Hemilepistus cristatus* etc).

Terrestrial Isopods are closely connected with the soil dwelling, their connection with the soil being the more close, the more xeromorphous is the station of the given species. There are terrestrial, closely connected with the soil forms also among the Amphipods (*Orchestia*) and Decapods.

Onychophora are typically airbreathing terrestrial forms, greatly susceptible to dessiccation and closely connected with soil habitats. The finding of fossil *Xenusion* and *Ayscheya* proves the Onychophora origin from the aquatic ancestors.

Closely adjusted to airbreathing are Myriapods and insects. Myriapods—more primitive Tracheata than the insects—are typically terrestrial (s.l.) forms, there are no aquatic forms among them. The inferior Myriapods (Symphyla and Pauropoda) are typically inhabitants of soil, litter and allied substrata. Among the Diplopoda the terrestrial forms are also prevalent; only in the tropical rain forests there are a few arboreal forms. Chilopods are closely connected with the soil, the

---

(1) Only the free living (non-parasitic) forms are considerated.

obligatory soil dwelling being characteristic to the more primitively segmentated Geophilomorpha. The more closely adjusted to the open habitats Schizotarsia are in many respects convergent to insects.

The inferior insect groups (Apterygota) are also characterized by the dwelling in soil and allied substrata. Only some of Apterygota are able to the existence out of the soil and similar shelters (e.g. Sminthuridae). Among the Pterygota closely connected with the soil and litter are such groups as Blattoidea, Grylloblattoidea.

More ancient ecological relations among the insects are exhibited in the oviposition sites. Even in Saltatoria group—the Acridoidea—having lost their connection with the soil—the development of uncleidoic eggs takes place always in the soil. The connections with the soil are evident in many of Tettigonoidea and Grylloidea (*Stenopelmatus, Schizodactylus*).

Embioidea are also soil dwellers. The retiring habits, especially in the early stages, and the connections with the soil are characteristic for termites, which require high air humidity.

Among the Hemimetabola the more closely adjusted to the open habitat in all the developmental stages are the Rhynchota. The close connection with soil in the nymphal period is observed in Cicadidae, the family laid as the base of the systematics of Homoptera.

In the subclass Holometabola the connection with the soil is also characteristic for the primitive forms in many orders, especially in larval stages, whereas the adults in Holometabola are more or less adjusted to the open habits. For example, among the beetles the larval stages of Adephaga and inferior Polyphaga are mainly soil dwellers. Even in such specialized families as the weevils, the more primitive forms are developing in soil (Adelognathi, Cleonini), whereas the more specialized Phanerognathi are developing in tissues of the foodplant or even on its surface (e.g., *Phytonomus*). Analogous examples may be given for other orders of Holometabola too.

The inferior Arachnids readily allied with the aquatic Xyphosura, though being common in arid localities, are closely connected with the soil and similar habitats.

The transition to the terrestrial life in molluscs owing to the presence of the shell, protecting terrestrial forms from the dessiccation, is not so closely connected with the soil. In the case of soil dwelling under the condition of the air saturation with water vapours, the shell of Gastropoda is reduced (Testacellidae, Limacidae).

The above review may be illustrated by the scheme of the transition from the aquatic to the terrestrial life. Fig. I shows the scheme of phylogenetical relations between the principal groups of Protostomian branch, leading to insects, which are represented in the ecological aspect.

The juvenile stages of insects, as the bulk of Apterygota, are usually connected with such habitats, where the danger of dessiccation is insignificant, in the primitive groups—with the soil.

Appreciation of the soil as independent environment (as the aquatic and terrestrial epigeion ones) allows to reconstruct the ecological conditions of the insect origin and evolution as following.

Transition of minute skinbreathing annelid—like aquatic animals to the inhabiting of soil and litter caused the development of Myria poda—characters. The example of the terrestrial Nereids shows the possibility of such a direction of the evolution. The limbs of the anterior part of the body are of principal importance for animal locomotion in the narrow passage—ways. Olygomerization of the segment quantity and tegmatization, the anterior part of the body acquiring locomotory function, have lead to the formation of the characters of « " Protohexapoda ", which had been living under the same conditions as their Myriapod—like ancestors.

The increased toughness of the integument (primarily connected with the mechanical function) lead to the formation of integuments protecting the organism from the rapid loss of water. The respiratory function transited from the whole skin surface to the specialized areas, which gave rise to the tracheae.

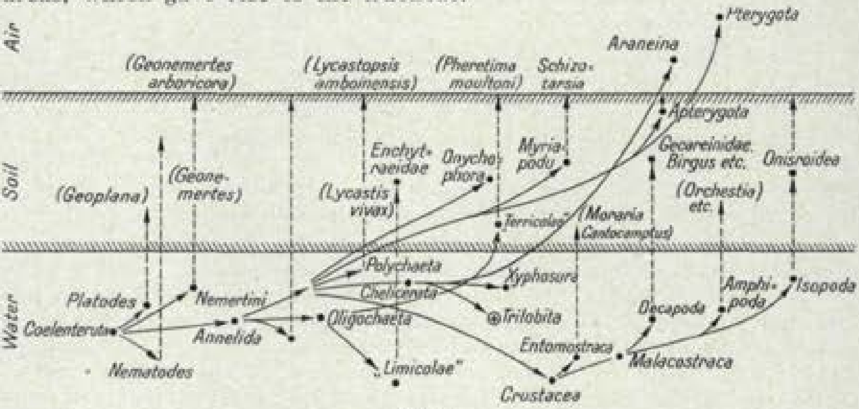

FIG. 1

Ecological aspect of the evolution of the Protostoman branch leading to insects.

The development of the integument inpermeability provided the emergence of the insect ancestors from soil and litter to the soil surface. This emergence, even in the case of creeping, facilitated the dispersal and mating.

The dispersal by creeping to the ancestors of the recent insects was substituted by jumping (as in the case of many recent Apterygots). Such mode of locomotion, complicated by the passive transportation by the wind, lead to the imperfect forms of flight, especially in the forms having lateral projections. Many wingless susceptible to dryness insects have, strongly developed paranotalia, which primarily function was protective (*Machilis, Carabus, Silpha*=larvae etc).

In the further evolution of the ancestors of Pterygota the adaptation of the adult stage to flight and epigeion habitation have taken place.

Thus the evolution from the primarily wingless to winged insects may be comprehensible. The adaptation of the adult stage to flight and life on the soil surface allow us to imagine two ways of the onthogenese evolution. In one case the juvenile stages tend to the adaptation to the open mode of life, under the same conditions as the adult forms—the way of Hemimetabola. In other case only the dispersing adult stage adjusted to the life on the soil surface whereas the feeding juveniles continued their hidden life,—which was peculiar to Protohexapoda. That is the way of Holometabola.

The thysanuroid oligopod form may be reckoned for the primarily one for the juveniles of both Hemimetabola and Holometabola.

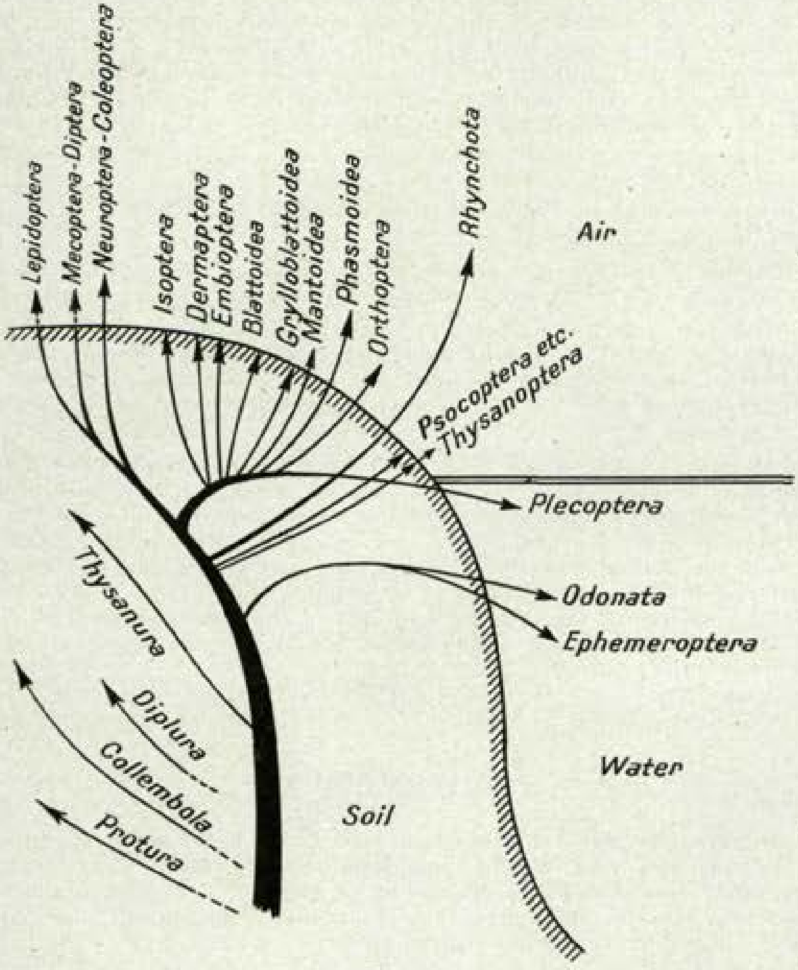

FIG. 2
Ecological aspect of the insect phylogeny.

The hypothese, that the insect ancestors had inhabited soil and similar substrata with the humid, saturated air enables us to understand the origin of insects with aquatic larvae. The larvae primarily inhabiting shore and bank soil or pebble could easily have transited to the amphibiotic and aquatic life (e.g. as *Osmylys chrysops* nowadays). So the Ephemeroptera larvae may be regarded as descendants of thysanuroid forms, which oligopod juvenile stage inhabited shore=pebble. Such an ecological way may explain the phylogeny of amphibiotical may—flies, dragonflies and caddis—flies, which larvae have a well—developed tracheal system.

The assumption of originally aquatic mode of life of insect larvae (according to Handlirsch, Lamèere and Martynov) makes unable the explanation of the appearence of the tracheal system. The appearance of tracheae is possible by the airbreathing only when, owing to the increase of the integument toughness or to the decrease of the surface/volume ratio, the skin respiration is unable to provide the gas exchange. Such an independent convergent appearance of the tracheae has taken place in different groups of Arthropods.

The ecological ways of the insect evolution, which were based on the appreciation of soil as a peculiar environment, described in detail by the author (1949), are represented in the scheme 2.

In this scheme as the principal habitat is regarded that one, in which the juvenil stage is developing, in as much the adult stage of Pterygota may be reckoned as having adjusted to the open habits.

The appreciation of soil and similar substrata as peculiar environment, contrary to epigeion terrestrial and aquatic ones, and the analysis of the environmental conditions in the soil enable us to ground with ecological data the phylogenetical schemes based on morphological material.

Almost complete absence of fossil intermediate forms between the aquatic and terrestrial invertebrate groups may be explained in the light of the above hypothese. The prevalent habitation of such forms in the soil makes the probability of their conservation quite negligible because the soil is a medium where the decomposition of organic residues, their mineralization and humification take place very rapidly. Therefore the use of the results of the palaentological studies for the solving of such problems as the origin of Myriapods and insects is quite restricted.

ZUSAMMENFASSUNG

Die Analyse der Umweltbedingungen beim Uebergang verschiedener Wirbellosen vom Wasser- zum Landleben im Laufe der Phylogenese zeigt, dass dieser Uebergang nur in solchem Lebensraum stattfinden kann, wo die Möglichkeit der Luftatmung nicht mit der Austrocknungsgefahr verbunden ist.

Solch' einen Uebergangslebensraum bietet der Boden für viele Gruppen von Wirbellosen dar.

Die Vertreter der wasserbewohnenden Wirbellosengruppen werden beim Uebergang zum Landleben zu Bodenbesiedlern oder sind mit dem Bodenleben eng verknüpft. Unter den Landtiergruppen sind die niederen Vertreter auch Boden- und Streubewohner.

Ihren physiologischen Merkmalen nach stehen viele Bodentier=arten den Wassertieren sehr nahe.

Die ökologische Auffassung ermöglicht das Korrigieren der phylogenetischen Schemata, die man früher fast ausschliesslich den morphologischen Angaben nach gebaut hat.

RÉSUMÉ

L'analyse des circonstances de la transition des groupes différents des invertébrés de la vie aquatique à la vie terrestre montre qu'une telle transition ne peut se produire qu'en passant un milieu dans lequel la possibilité de la respiration de l'oxygène aérien n'entraine pas un danger de dessiccation.

Un tel milieu au cours de la phylogénèse est représenté pour plusieurs groupes d'invertébrés par le sol.

Les représentants des groupes aquatiques en passant à la vie terrestre habitent le sol ou sont liés avec lui ; parmi les groupes terrestres des invertébrés les inférieurs habitent aussi le sol. Par leurs caractères physiologiques plusieurs membres de la faune du sol se rapprochent beaucoup des organismes aquatiques.

La conception écologique permet de corriger les schémas phylogénétiques basés autrefois uniquement sur les données morphologiques.